

Comparative Life Histories and Predation Types: Are *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae) Similar Type II Selective Predators of Spider Mites?

B. A. CROFT, L. N. MONETTI,¹ AND P. D. PRATT

Department of Entomology, Oregon State University, Corvallis, OR 97331-2907

Environ. Entomol. 27(3): 531-538 (1998)

ABSTRACT Both *Neoseiulus californicus* (McGregor) and *N. fallacis* (Garman) have been rated a type II selective predator of spider mites that feeds more on spider mites than pollen or insects. We assessed this predation rating or an alternative hypothesis that *N. californicus* is more of a generalist predator than *N. fallacis*. In tests, reproduction was equal or greater for *N. californicus* than *N. fallacis* when each was held separately with excess *Tetranychus urticae* Koch, *Panonychus ulmi* (Koch), *Frankliniella occidentalis* (Pergrande), or maize pollen, but it was less when with *Aculus schlectendali* Nalepa or *Oligonychus ilicis* (McGregor). *N. californicus* had other traits more like those of a generalist predator—adult females had shorter dorsocentral setae and moved farther on a plant but less often and for less distance between plants. *N. californicus* nymphs fed more either intraspecifically and interspecifically on phytoseiid eggs, but adult females of both species fed similarly on eggs of either phytoseiids. Larval feeding was less for *N. californicus* but nymphal feeding drive was alike for both species. Of 17 traits that were tested, 11 indicated more of a generalist role for *N. californicus*; 6 traits did not differ between species, and none indicated that *N. californicus* was more of a specialist predator of spider mites than *N. fallacis*. *N. fallacis* clearly is a specialist type II species, but a rating between specialist II and generalist III is needed for *N. californicus*. Traits of immatures were more discriminating than traits of female adults in this study; both trait types should be included in predation rating systems.

KEY WORDS Eriophyidae, Thripidae, Tetranychidae, generalist predator, specialist predator, alternate foods

A CLASSIFICATION SYSTEM of life style or predation types for phytoseiid mites has been proposed by McMurtry and Croft (1997). It includes 4 types spanning from highly specialized (type I) as predators of spider mites to more generalized feeding types (type IV). Ratings were based mostly on feeding specialization of adult females but other life history traits were considered. Type I is a specialized predator of *Tetranychus* species of spider mites that spin much webbing, of which the *Phytoseiulus* species are representative. Type II is a selective predator that often associates with spider mites that produce less webbing and is represented by *Galendromus*, some *Neoseiulus*, and a few *Typhlodromus* species. Type III is a generalist that feeds on many mites and pollens and is represented by some *Neoseiulus* and most *Typhlodromus* and *Amblyseius* species. Type IV is a generalist feeder on mites, but a specialist feeder on pollen; it is represented by most *Euseius* species. Recently, we had reason to compare 2 similar species, *Neoseiulus californicus* (McGregor) and *N. fallacis* (Garman), to see how well they fit these predation ratings according to the traits of adult female and immature life stages.

Neoseiulus californicus is a cosmopolitan mite of subtropical and temperate regions. It has an extensive distribution in South America where it ranges from southern Argentina and Chile to Ecuador and Colombia and from Peru to Brazil (CIAT 1995, McMurtry and Croft 1997). It also occurs in southern Europe and California (McMurtry and Croft 1997). It occurs on many plants such as citrus, pomes, strawberry, grape, cassava, soybean, and vegetables (McMurtry and Croft 1997). On some crops, it has evolved strains that are highly resistant to pesticides; this adaptation allows *N. californicus* to persist more readily in IPM systems where pesticides are used selectively and in moderation (Croft 1990).

The life history of *N. californicus* was 1st studied in the 1970s (Swirski et al. 1970, Ma and Laing 1973) but its role as a predator of spider mites has been uncertain. It was thought to be a specialist predator on citrus, based on peak population levels and its seasonal dynamics with the spider mite, *Panonychus citri* (McGregor) (McMurtry 1992). However, Swirski et al. (1970) and Castagnoli and Liguori (1991) previously had found that it could readily feed and reproduce on pollens. This reflects more of a generalist role. McMurtry and Croft (1997) rated *N. californicus* and *N. fallacis* both as type II predators of spider mites.

¹ Current address: University of Mar del Plata, Mar del Plata, Argentina.

This rating includes species that feed more on spider mites than on pollen, insects, or other foods. Comparative life history studies with other phytoseiids are more common for *N. fallacis* than for *N. californicus* (Croft and Croft 1993, 1996; Zhang and Croft 1994, 1995a, 1995b; Croft et al. 1996; McMurtry and Croft 1997).

In a series of studies (Monetti and Croft 1997a, b; Pratt et al. 1998; the present study), single strains of *N. fallacis* and *N. californicus* were tested for selected aspects of setal length, reproduction, development, feeding, food types, intraplant or interplant dispersal, and intraspecific or interspecific predation. Most factors that were compared were those that were proposed to define type II and type III predation types (McMurtry and Croft 1997). These 2 species were studied with regard to their roles as predators because they were being considered for use in inoculative release programs on ornamental and several crop plants (Strong and Croft 1995, Pratt et al. 1998). Both are similar in setal characteristics, but they are distinct taxonomically, and only haploid males are produced between them when mating occurs in the laboratory (Monetti and Croft 1997a). Throughout our study, 2 hypotheses were being considered—that both species indeed are similar type II specialist predators of spider mites or that *N. californicus* is more of a generalist predator than is *N. fallacis*.

Materials and Methods

Laboratory tests were conducted in environmental chambers at $25 \pm 1^\circ\text{C}$ and $80 \pm 10\%$ RH except when population assessments were made. Greenhouse tests were conducted in environmental rooms at 26:21 (night:day) $\pm 5^\circ\text{C}$, $75 \pm 10\%$ RH, and a photoperiod of 16:8 (L:D) h. Except in 1 case, all predators that were used came from long-established cultures that were maintained on small-tray units (Scriven and McMurtry 1971). Predators were fed mixed life stages of the twospotted spider mite, *Tetranychus urticae* (Koch), at regular intervals (daily or 3/wk). For 1 of 3 studies of nymphal feeding drive (see below), predators were mass-produced by feeding on *T. urticae* that were reared on lima bean plants grown in a greenhouse using the same environmental controls and conditions as described above (Strong and Croft 1995).

Reproduction and Development. Tests for each species always were conducted simultaneously, but on separate arenas or plants—1 deutonymph + 1 adult male were placed on a waterproofed arena (2.5 by 2.5 cm) made of construction paper and ringed with Tanglefoot (Tanglefoot, Grand Rapids MI 49504) to prevent mite escapes. Each arena with predator mites was provisioned with excess mixed life stages of *T. urticae*, replaced daily. After mites were mated, egg and active immatures that were produced were counted daily for 7 d in 10 replicates. In a 2nd test, methods were as before except 3 mated adult females of mixed ages were added per arena. In a 3rd test in a greenhouse, 50 or 100 mated adult females were placed on a centrally located leaf either on a bean

plant system (0.3 or 0.7 m diameter) or on a basal leaf of a 1-m apple shoot (Pratt et al. 1998). Eggs and the immature life stages that were produced and their locations on leaves of plants were assessed daily for 10 d (5 replicates per species). Cumulative mean densities of immature mites that were produced were compared by repeated-measures analysis of variance (ANOVA) and Fisher protected least significant difference (LSD) test (Hintze 1995).

Adult female predators were transferred to bean plants and rates of development of offspring from egg to deutonymph stage were compared after 2 and 4 d for eggs and 6 and 8 d for deutonymphs (Pratt et al. 1998). All tests were terminated after 8 d because new adult females developed soon thereafter and they could not be separated or identified from original adult mites. To test rates of development, mean levels of eggs and deutonymphs that eclosed at each time period were compared using repeated-measures ANOVA and Fisher LSD tests (Hintze 1995).

Feeding and Survival on Provisioned Foods. Tests were conducted either on 2.5 paper arenas (2.5 by 2.5 cm) or similarly sized apple leaf arenas (midrib up) that were ringed by water-soaked cotton. Excess amounts of mixed life stages of either *T. urticae*, *Panonychus ulmi* (Koch), *Oligonychus ilicis* (McGregor), *Aculus schlechtendali* Nalepa, *Franklinella occidentalis* (Pergrande) (Insecta: Thripidae), or fresh maize pollen were added and replaced daily. Amounts of provisioned foods were varied according to daily consumption rates. For spider mites, the amounts added each day were 30–50 mixed life stages; for rust mites, it was 100–200 of all stages; for thrips it was from 5 to 10 immatures, and for corn pollen it was ≈ 500 –1,000 pollen grains. Apple leaf arenas were used as substrate for prey that quickly moved into barriers on paper arenas such as *P. ulmi* or *A. schlechtendali*. The apple leaf substrate (same size and shape as paper arenas) also was used in tests to increase the relative humidity and keep pollen grains turgid. Three adult female predators were added per arena (8 replicates per species). At the same time daily, adult female loss from arenas, activity (walking during a 1-min period of observation) and the number of eggs and active immature progeny that were produced were measured for 7 d. This time span was near the maximum before new female adults appeared on rearing units. Mean responses to each food types between the 2 phytoseiids were compared with a Student *t*-test and comparisons among food types within species were made using an ANOVA and Fisher LSD test (Petersen 1985).

Intra- and Interspecific Predation by Adult Females. Single, mated adult females of each species (15 replicates per treatment) were 1st held for 24 h without food. These mites then were placed in a 2.5-cm cage (70 μm cell strainer, Benton Dickinson, Lincoln Park, NJ) (Croft and Croft 1993) and held for 2 d with 10 new (<24 h old) phytoseiid eggs. Use of new eggs allowed predators to pierce the egg chorion before a larval integument was laid down inside the egg. It was thought that older eggs might limit predation to some degree. Treatments were each *Neoseiulus* species pro-

Table 1. Egg and active immature production of *N. fallacis* and *N. californicus* when held with excess mixed life stages of *T. urticae* in different test types

Test type	<i>N. fallacis</i>	<i>N. californicus</i>	<i>N. fallacis</i> / <i>N. californicus</i>	<i>P</i> ^a	Reference
Egg production					
X mating	1.29 ^b	2.19	0.58	0.000	Monetti and Croft 1997
Prey types	3.44 ^c	3.45	1.00	0.771	Current study
Small-bean plant	4.03 ^d	3.59	1.27	0.626	Pratt et al. 1998
Large-bean plant	3.50 ^d	2.75	1.13	0.166	Pratt et al. 1998
Larva and nymph production					
Prey types (larvae and nymphs)	1.64 ^e	2.08	0.78	0.229	Current study
Small-bean plant nymphs	3.62 ^f	3.19	1.13	0.498	Pratt et al. 1998
Large-bean plant nymphs	2.48 ^g	3.64	0.68	0.014	Pratt et al. 1998

^a ANOVA *P* and degrees of freedom in reference; current study, *df* = 5, 35.

^b Cumulative eggs/♀/d for 4.5 d after mating.

^c Cumulative eggs/♀/d for 7 d after adult transfer (Table 2).

^d Cumulative eggs/♀/d for 6 d after transfer of adult.

^e Cumulative mixed nymphs/♀/d for 8 d after transfer of adults.

^f Cumulative protonymphs/♀/d for 8 d after transfer of adults.

^g Cumulative deutonymphs/♀/d for 8 d after transfer of adults.

visioned either with eggs of its own species or those of the other. Counts were taken at the same time each day for the number of eggs eaten and adult female activity (ambulation) during 1 min of observation per day. Mean response data for each attribute were compared within and between species by an ANOVA and Fisher protected LSD test (Petersen 1985).

Results

Reproduction and Development. Cumulative means of eggs or active immatures that were produced either were not different between species or they were slightly greater for *N. californicus* ($P < 0.05$ in 2 of 7 tests; Table 1). However, if statistical results were not considered, levels were slightly greater for *N. fallacis* in 2 of 4 tests for eggs and 1 of 3 for active immature stages. Overall, data suggested that reproductive rates were very similar for these species. Although mortality or dispersal could have differed between the 2 species and thus affected tests, no loss rate differences were seen. Considering the number of tests that were run, it is unlikely that a common factor was influencing tests similarly. Eggs oviposited by predators were not removed from arenas so that immatures that developed could be estimated without disturbance. Results may have differed if immatures had been transferred daily and development had been followed for the entire period of reproduction (Helle and Sabelis 1985). It is known, for example, that both species will oviposit more eggs during the 1st few days after transfer to a new arena than later after colonization has occurred (unpublished data). However, no studies have been done to see if either species has a greater oviposition rate during this period relative to its overall rate of reproduction.

In large-plant studies, eggs of *N. californicus* were not more common on day 2 ($P = 0.131$; *df* = 1, 8; $F = 2.83$) or day 4 ($P = 0.867$; *df* = 1, 8; $F = 0.03$) but deutonymphs were on day 6 ($P = 0.031$; *df* = 1, 8; $F = 6.83$) and almost were on day 8 ($P = 0.073$; *df* = 1, 8; $F = 4.26$) (Fig. 1). Day 6 was the 1st on which

enough deutonymphs were present to do statistical tests for both species, but a few *N. californicus* deutonymphs consistently were seen a day earlier than for *N. fallacis* (unpublished data, Monetti and Croft 1997b). *N. californicus* may develop slightly faster than *N. fallacis*, but developmental rates must be very similar. Similar developmental rates between these species also were seen in other studies with immatures (Monetti and Croft 1997a, b).

Feeding and Survival on Provisioned Foods. Differences in adult female survival, activity, oviposition per female per day, cumulative eggs per female, and cumulative immatures per 3 female adults were observed when each phytoseiid was held with several spider mites, an eriophyid, maize pollen, or thrips immatures (Table 2). Generally, both mites survived and reproduced less when provisioned and feeding only on active stages (eggs could not be pierced) of the nonweb-spinning spider mites, *P. ulmi* and *O. ilicis* (compared with *T. urticae* as controls). Both phytoseiids had high survival when provisioned with *P. ulmi*, but only moderate reproduction. Both of these species can control *P. ulmi* in the field (McMurtry and Croft 1997). When held with *O. ilicis*, survival and reproduction were much less for *N. californicus* and somewhat less for *N. fallacis* than when with *T. urticae* or *P. ulmi*. In the field, poor control was seen when *N. californicus* was released in inoculative release experiments to control *O. ilicis* on ornamentals, whereas *N. fallacis* gave good control (Pratt et al. 1998). Differences also were seen when both predators were held only with the eriophyid apple rust mite, *A. schlechtendali* (Table 3). *N. fallacis* reproduced at moderate rates, but *N. californicus* did only at very low rates. *N. fallacis* did not numerically increase rapidly when held only with *A. schlechtendali* in apple plots in the field (Croft and Hoying 1976); *N. californicus* also did not reproduce extensively when held only with a citrus eriophyid (Swirski et al. 1970). Neither of these phytoseiids seems well adapted to feed, reproduce, and provide biological control of eriophyids or to use them as a major food source as done by several other

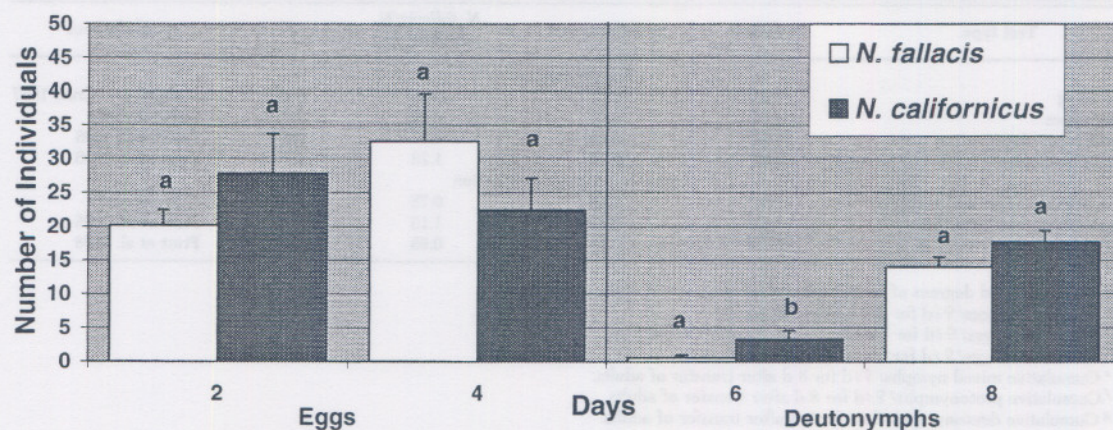
Life Stage of *N. californicus* and *N. fallacis*

Fig. 1. Mean number (+SE) of protonymphs or deutonymphs of *N. californicus* or *N. fallacis* found on 4 sampling dates in large bean plant experiments (from analysis of unpublished data that were collected in studies reported by Pratt et al. 1998).

phytoseids (McMurtry and Croft 1997, Croft et al. 1998).

With regard to nonmite foods, feeding on thrips enhanced survival of both species of predaceous mites, but more reproduction was seen for *N. californicus* than for *N. fallacis* (Table 2). In these feeding tests with immature thrips, adult females of *N. fallacis* often looked flat, starved, and without an egg in the abdomen while *N. californicus* looked round, full, and gravid. It is not known if these 2 mites exhibit predation

widely on other insects, but among other phytoseids, entomophagy on scales, psocids, lepidopterans, Collembola, and probably many other types of small species can occur (McMurtry and Croft 1997, Croft et al. 1998).

In past studies, Swirski et al. (1970) and Castagnoli and Liguori (1991) reported successful development and reproduction by *N. californicus* when provided with several pollens. Similar studies with *N. fallacis* have been more limited (Ahlstrom and Rock 1973),

Table 2. Survival, activity, oviposition, and progeny for *N. fallacis* and *N. californicus* during 7 d when held with unlimited amounts of food, replaced daily

Predator or food type	% ♀ survival ^a	% ♀ active ^b	Eggs/♀/d ^c	Cumulative eggs ^d	Cumulative progeny ^e
<i>N. fallacis</i>					
<i>T. urticae</i> ^f	0.83ab	48.2a	3.44c	58.0c	33.2b
<i>P. ulmi</i> ^f	1.00b	74.6bc	1.43b	30.2b	21.8b
<i>O. ilicis</i> ^f	0.55a*	82.6bc***	1.40b**	20.3b***	16.3b
<i>A. schlechtendali</i> ^g	0.83ab***	90.2bc*	1.68b*	29.8b***	23.2b**
Corn pollen	0.94b	70.9b	1.58b	29.7b	23.2b
<i>F. occidentalis</i> ^h	0.67ab	92.6c	0.10a***	2.2a***	0.5a***
F (P values)	0.0139	<0.0001	0.0001	<0.0001	0.0003
<i>N. californicus</i>					
<i>T. urticae</i> ^f	0.72b	58.3NS	3.45c	54.5d	3.33c
<i>P. ulmi</i> ^f	1.00c	81.7	2.01b	36.5c	23.0b
<i>O. ilicis</i> ^f	0.27a*	49.2***	0.87a**	9.3a***	13.8a
<i>A. schlechtendali</i> ^g	0.33a***	70.7*	0.83a*	9.7a***	6.2a**
Corn pollen	0.89bc	75.7	1.18a	22.5b	34.2c
<i>F. occidentalis</i> ^h	0.44a	74.3	1.12a***	12.8a***	4.8a***
F (P values)	<0.0001	0.1736	<0.0001	<0.0001	>0.0001

Means for species in column that are followed by the same letter are not significantly different ($P \leq 0.05$, Fisher LSD test); see significance of ANOVA F below results in each column, $df = 5, 35$ in each test of food types. Means without asterisk are not significantly different between predators for that attribute and food. *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$ (Students t -test).

^a After 7 d on arenas.

^b Ambulating per 1-min observation per day.

^c Mean cumulative eggs per female per day.

^d Mean cumulative eggs in 7 d per 3 female adults.

^e Mean cumulative progeny in 7 d per 3 female adults.

^f Acari: Tetranychidae.

^g Acari: Eriophyidae.

^h Insecta: Thysanoptera: Thripidae.

Table 3. Intra- and interspecific predation by adult female *N. californicus* and *N. fallacis* held 10 d with 10 (<24 h) phytoseiid eggs, replaced daily

Adult:eggs	n	Eggs eaten/d	% Adult activity frequency
<i>N. californicus</i> : <i>N. californicus</i>	15	3.47a	0.83NS
<i>N. californicus</i> : <i>N. fallacis</i>	15	4.53ab	0.80
<i>N. fallacis</i> : <i>N. fallacis</i>	15	3.13a	0.87
<i>N. fallacis</i> : <i>N. californicus</i>	15	5.40b	0.77

ANOVA significance of *F* values and degrees of freedom for eggs eaten per day were $P < 0.017$, $df = 3, 42$; adult female activity were $P = 0.754$, $df = 3, 42$; means followed by the same letter are not significantly different, $P = < 0.05$; Fisher LSD test; NS, non-significant *F* test.

but reports of limited mass rearing (Zhang and Li 1989) verifies that some pollen types can support development and reproduction. In our studies, both species survived and reproduced at high rates on fresh maize pollen (Table 2). Although pollen consumption has been reported before for these 2 mites, levels of reproduction usually have not been as high as was seen here (Table 2). Part of the difference may have been related to the pollen species that was provided (Swirski et al. 1970) or its condition. To our knowledge, the impact of pollen turgidity or freshness has not been studied with either of these 2 phytoseiids and not to any great extent among phytoseiids in general.

Intra- and Interspecific Predation by Adult Females. When held with only phytoseiid eggs, feeding levels by adult female *N. fallacis* and *N. californicus* were less different than for their nymphs (Monetti and Croft 1997b). Female adults of both species fed on eggs of their own species at about the same level (Table 3). Female adults of both species fed at somewhat higher levels on each other's eggs than on their own, but only for *N. fallacis* was the difference significant ($P = 0.05$). Between the 2 species, rates of feeding on each other's eggs were not different. Feeding by nymphs of *N. californicus* on eggs of either species was significantly greater than for *N. fallacis* nymphs, but nymphs of *N. fallacis* fed much less on eggs of their own species than on eggs of *N. californicus* (Monetti et al. 1997b). In all tests of intraspecific and interspecific predation with adult females, there were no differences in activity levels between species, and rates of activity were very high compared with well-fed mites (Table 3; Croft et al. 1996). This may indicate that adult females of either species were relatively hungry when present only with phytoseiid eggs.

Data for intraspecific and interspecific predation for these 2 mites and for *N. fallacis* and 3 other species when feeding on all life stages of each other (Croft and Croft 1993, Croft et al. 1996, current study) give perspective to observations made while rearing them continuously. Under identical rearing conditions, *N. fallacis* can be sustained at higher densities on small-tray units (Scriven and McMurtry 1971) than *N. californicus*; both can be maintained at much higher levels than *Metaseiulus occidentalis* (Nesbitt), *Amblyseius andersoni* (Chant), and *Typhlodromus pyri* (Scheuten) (unpublished data). Both *Neoseiulus* species feed less on

their own egg and active immature life stages than do the other 3 species (Croft and Croft 1993, 1996; Croft et al. 1996). *N. californicus* is somewhat more cannibalistic than *N. fallacis*, especially in the nymphal stages. This factor probably accounts for most of the differences that are seen in population levels of each species that can be maintained on rearing units in the laboratory.

Discussion

Other Traits. Sabelis and Bakker (1992) proposed that specialized predators of spider mites have longer dorsal setae to facilitate movement in webbed-over colonies of spider mites; generalist predators have shorter setae and have more difficulty in moving in spider mite webbing. Dorsal setal length relationships are used in keys to discriminate these species (Schuster and Pritchard 1963). These differences held for the strains studied here—*N. fallacis* had dorsocentral setae that exceeded the distances between their bases; *N. californicus* did not (unpublished data; Fig. 2). These traits can be used to separate mixed samples of these 2 predaceous mites under a phase-contrast microscope at 100–200 \times magnification (Pratt et al. 1998).

In movement studies (Pratt et al. 1998), *N. californicus* moved farther out from a central release point in bean or apple plant systems than did *N. fallacis*. This difference affected the degree and pattern of biological control that each species provided within a plant or in a contiguous plant system. Whereas *N. fallacis* tended to move out slowly and suppressed *T. urticae* locally, the dispersive adult females and progeny of *N. californicus* suppressed spider mites on all leaves in a more even way. Eggs and active immatures stages of these mites were less dispersed than adult females within plants but differences between species still were present. Immatures of *N. californicus* were more dispersed. Both a more widespread placement of eggs by females and greater movements of protonymphs and deutonymphs contributed to the differences seen in spatial distributions of immatures (unpublished data, Pratt et al. 1998). In studies of dispersal between isolated plants (Pratt et al. 1998), *N. fallacis* moved earlier, at higher prey levels, and farther than *N. californicus*. Different responses to prey densities, a stance behavior that may influence takeoff and differences in buoyancy because of setal differences, were suspected to account for differences in the timing and distance of dispersal. Greater interplant dispersal would be expected for a specialist predator (*N. fallacis*) that must find aggregated patches of a colonizing mite like *T. urticae* (Brandenburg and Kennedy 1987).

Phytoseiids with larvae that feed more tend to have nymphs that feed less, and may be more specialized predators of spider mites (Croft and Croft 1993, McMurtry and Croft 1997; see exceptions in Zhang and Croft 1994). In our studies, *N. fallacis* larvae fed only slightly, but significantly more than *N. californicus* larvae; also larvae of *N. fallacis* were more active and moved farther, but feeding drives of nymphs were

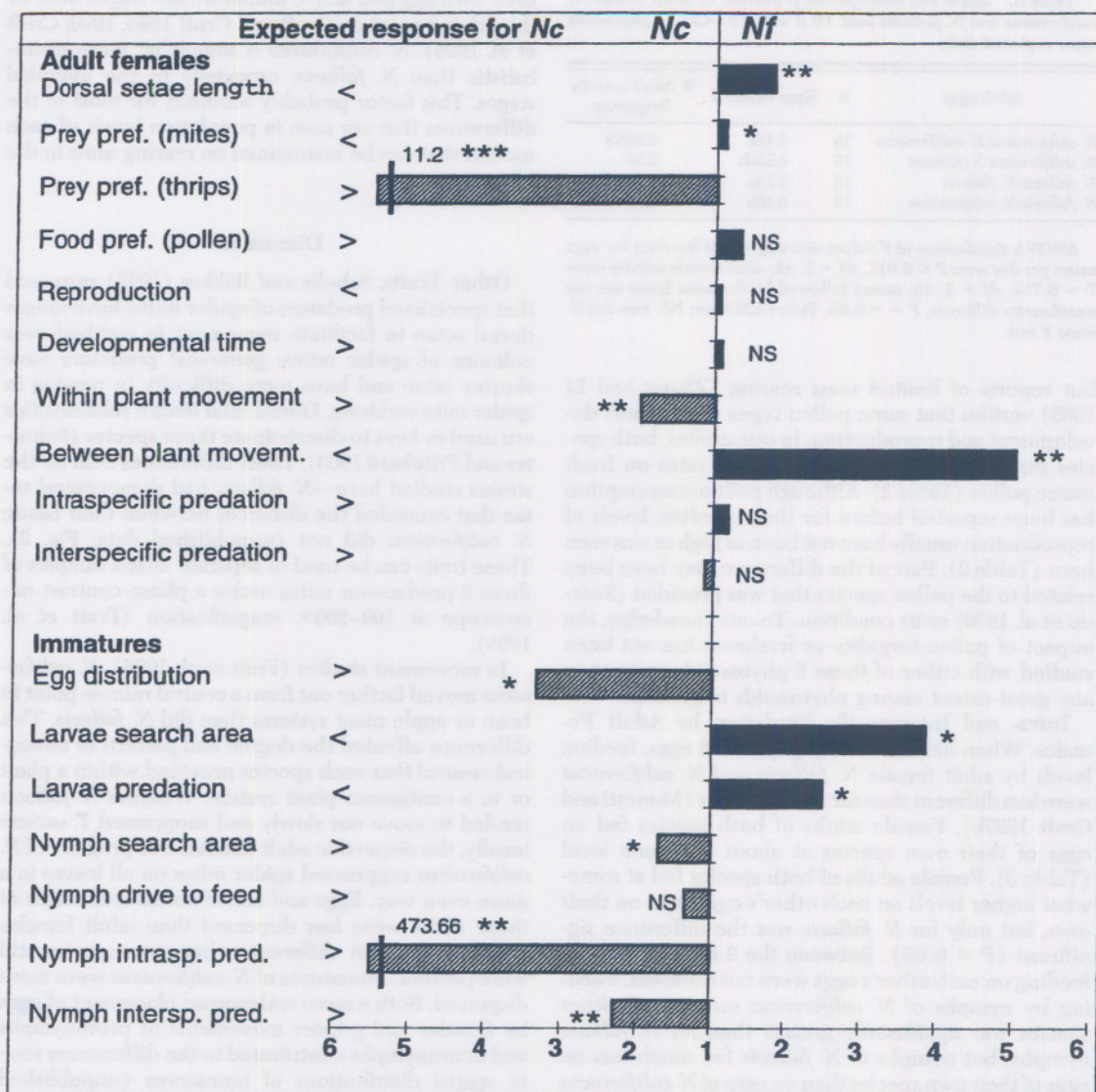


Fig. 2. Expected and observed results to evaluate if *N. californicus* (Nc) is more of a generalist type III predator of tetranychid mites than *N. fallacis* (Nf). From a series of studies by Monetti and Croft (1997a, b) and Pratt et al. (1998) and current study, *, $P \leq 0.5$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

similar (Monetti and Croft 1997b). Larval feeding rates of either species were much less than for some phytoseiids. Larval feeding of *M. occidentalis* is near 100% because this stage must feed to develop onward (Croft and Croft 1993). For either *Neoseiulus* species, larval feeding rates may be too low to result in any differences in nymphal feeding drive.

Application to Predation Models. McMurtry and Croft (1997) proposed traits of mostly adult females to describe 4 predation types ranging from highly specialized to generalized (I–IV). A type II rating for *N. fallacis* is well established from tests with other type IIs (*M. occidentalis*) and type IIIs (*T. pyri*, *Amblyseius*

andersoni) (Croft and Croft 1993, 1996; Croft and Zhang 1994, Zhang and Croft 1994, 1995a, 1995b; Croft et al. 1995a, 1995b, 1996). Similar comparative data for *N. californicus* and other species are less available (McMurtry and Croft 1997). After comparing their attributes, we rejected the proposal that *N. californicus* and *N. fallacis* are similar type II specialized predators of spider mites (Monetti and Croft 1997a, b; Pratt et al. 1998, herein) in favor of the hypothesis that *N. californicus* is more of a generalist predator of these pests. Observed versus expected results to verify this premise are plotted as ratios of the data in Fig. 2 (specific units of comparison are described more fully

in Monetti and Croft 1997a, b; Pratt et al. 1998). Large differences occurred for cannibalism by nymphs (*N. californicus*), reproduction on thrips (*N. californicus*) and interplant dispersal (*N. fallacis*). Data confirmed the expected for 11 traits and no difference for 6 traits ($P \leq 0.05$). None of the 17 traits indicated that *N. californicus* was a more specialized predator of spider mites than *N. fallacis*. More traits of immature stages (6 of 7; Fig. 2) were discriminating than of adult females (5 of 10; Fig. 2). The largest difference was a trait for an immature stage, not an adult female (intra-specific predation by nymphs; Fig. 2).

Predation ratings reflect a continuum of types (McMurtry and Croft 1997). *N. californicus* should be rated between a type II and III, or an intermediate rating is needed (see similar needs to adjust ratings for many type III species based on food preferences differences; Croft et al. 1998). Beyond this change, these studies showed examples of tests that can be used to evaluate predation types and adult and immature traits. All traits that were examined in this study may not prove discriminating when many species are compared, but they indicate some types of analyses that may be useful. All such traits need more testing among species (see data for other commonly studied phytoseiid species and traits for which data may be available in Croft et al. 1998) and within a species. For example, traits of intra- or interspecific predation can involve each active life stage feeding on all other life stages (Croft and Croft 1996; Croft et al. 1995b, 1996). In these studies, only predation by adult females or nymphs on eggs was evaluated. Such more extensive and intensive studies will help define predation types and roles of individual species in whole complexes of phytoseiids.

Acknowledgments

We thank D. Slone and L. Coop for help with statistics and J. A. McMurtry and G. W. Krantz for review of the manuscript (Oregon State University). L.M. was funded by Consejo Nacional De Investigaciones Cientificas Y Tecnologicas, Buenos Aires, Argentina. This is Article 11,305 of the Oregon Agricultural Experiment Station.

References Cited

- Ahlstrom, K. R., and G. C. Rock. 1973. Comparative studies on *Neoseiulus fallacis* and *Metaseiulus occidentalis* for azinphosmethyl toxicity and effects of prey and pollen on growth. *Ann. Entomol. Soc. Am.* 66: 1109–1113.
- Brandenburg, R. L., and G. G. Kennedy. 1987. Ecological and agricultural considerations in management of twospotted spider mite (*Tetranychus urticae* Koch). *Agric. Zool. Rev.* 2: 185–236.
- Castagnoli, M., and M. Liguori. 1991. Laboratory observations on duration of copulation and egg production of 3 phytoseiid species fed on pollen, pp. 231–239. In R. Schuster and P. W. Murphy [eds.], *The Acari: reproduction, development and life history strategies*. Chapman & Hall, London.
- [CIAT]. 1995. Cassava program annual report–1994, p. 47. In International Center of Tropical Agriculture, Cali, Colombia.
- Croft, B. A. 1990. *Arthropod biological control agents & pesticides*. Wiley, New York.
- Croft, B. A., and M. B. Croft. 1993. Larval survival and feeding by immature *Metaseiulus occidentalis*, *Neoseiulus fallacis*, *Amblyseius andersoni* and *Typhlodromus pyri* (Acari: Phytoseiidae) on life stages of *Tetranychus urticae* Koch and phytoseiid larvae. *Exp. Appl. Acarol.* 17: 685–693.
1996. Intra- and interspecific predation among adult female *Metaseiulus occidentalis*, *Typhlodromus pyri*, *Neoseiulus fallacis* and *Amblyseius andersoni*. *Environ. Entomol.* 25: 853–858.
- Croft, B. A., and S. A. Hoying. 1977. Competitive displacement of *Panonychus ulmi* (Koch) by *Aculus schlechtendali* Nalepa in apple orchards. *Can. Entomol.* 109: 1025–1034.
- Croft, B. A., and Z.-Q. Zhang. 1994. Walking, feeding and interaction of larvae of *Metaseiulus occidentalis*, *Typhlodromus pyri*, *Neoseiulus fallacis* and *Amblyseius andersoni* held with and without eggs of *Tetranychus urticae*. *Exp. Appl. Acarol.* 18: 567–580.
- Croft, B. A., S. S. Kim, and D. I. Kim. 1995a. Leaf residency and interleaf movement of four phytoseiid mites (Acari: Phytoseiidae) on apple. *Environ. Entomol.* 24: 1344–1351.
- 1995b. Absorption and cannibalism: do phytoseiids conserve egg resources when prey densities decline rapidly? *Exp. Appl. Acarol.* 19: 347–356.
1996. Intra- and interspecific predation on four life stage groups by adult females of *Metaseiulus occidentalis*, *Typhlodromus pyri*, *Neoseiulus fallacis* and *Amblyseius andersoni*. *Exp. Appl. Acarol.* 20: 435–444.
- Croft, B. A., J. A. McMurtry, and H. Luh. 1998. Do literature records of predation reflect food specialization among species and predation types of phytoseiid mites (Acari: Phytoseiidae)? *Exp. Appl. Acarol.* (in press).
- Helle, W., and M. W. Sabelis. 1985 [eds.]. *Spider mites: their biology, natural enemies and control*. Elsevier, Amsterdam.
- Hintze, J. L. 1995. *Number Cruncher Statistical System, 6.0 users manual*. NCS, Kaysville, UT.
- Ma, W. L., and J. E. Laing. 1973. Biology, potential for increase and prey consumption of *Amblyseius chilensis* (Dosse) (Acarina: Phytoseiidae). *Entomophaga* 18: 47–60.
- McMurtry, J. A. 1992. Dynamics and potential impact of 'generalist' phytoseiids in agroecosystems and possibilities for establishment of exotic species. *Exp. Appl. Acarol.* 14: 371–382.
- McMurtry, J. A., and B. A. Croft. 1997. Life styles of phytoseiid mites and their roles as biological control agents. *Annu. Rev. Entomol.* 42: 291–321.
- Monetti, L. N., and B. A. Croft. 1997a. Mating, cross-mating and related behaviors of *Neoseiulus californicus* and *N. fallacis* (Acari: Phytoseiidae). *Exp. Appl. Acarol.* 20: 67–71.
- 1997b. *Neoseiulus californicus* (McGregor) and *N. fallacis* (Garman): larval response to prey-humidity treatments, nymphal feeding drive and nymphal predation on phytoseiid eggs. *Exp. Appl. Acarol.* 20: 225–234.
- Petersen, R. G. 1985. *Design and analysis of experiments*. Dekker, New York.
- Pratt, P. D., L. N. Monetti, and B. A. Croft. 1998. Within and between plant dispersal and distributions of adult females and immatures of *Neoseiulus californicus* and *N. fallacis* in bean and apple plant systems. *Environ. Entomol.* 27: 148–153.
- Sabelis, M. W., and F. M. Bakker. 1992. How predatory mites cope with the web of their tetranychid prey: a

- functional view of the dorsal chaetotaxy in the Phytoseiidae. *Exp. Appl. Acarol.* 16: 203-225.
- Schuster, R., and A. E. Pritchard. 1963. Phytoseiid mites of California. *Hilgardia* 34: 191-285.
- Scriven, G. T., and J. A. McMurtry. 1971. Quantitative production and processing of tetranychid mites for large-scale testing or predator production. *J. Econ. Entomol.* 64: 1255-1257.
- Strong, W. B., and B. A. Croft. 1995. Inoculative release of phytoseiid mites into the rapidly expanding canopy of hop for control of *Tetranychus urticae* Koch. *Environ. Entomol.* 24: 446-453.
- Swirski, E., S. Amitai, and N. Dorzia. 1970. Laboratory studies of the feeding habits, post-embryonic survival, and oviposition of the predaceous mites *Amblyseius chilensis* Dosse and *Amblyseius hibisci* Chant (Acarina: Phytoseiidae) on various kinds of food substances. *Entomophaga* 15: 93-106.
- Zhang, N. X., and Y. X. Li. 1989. An improved method of rearing *Amblyseius fallacis* (Acari: Phytoseiidae) with plant pollen. *Chin. J. Biol. Control* 5: 149-152.
- Zhang, Z.-Q., and B. A. Croft. 1994. A comparative life history study of immature *Neoseiulus fallacis*, *Amblyseius andersoni*, *Metaseiulus occidentalis*, and *Typhlodromus pyri* (Acari: Phytoseiidae) with a review of larval feeding patterns in the family. *Exp. Appl. Acarol.* 18: 635-657.
- 1995a. Intraspecific competition in immature *Amblyseius fallacis*, *Amblyseius andersoni*, *Typhlodromus occidentalis* and *Typhlodromus pyri* (Acari: Phytoseiidae). *Exp. Appl. Acarol.* 19: 65-77.
- 1995b. Interspecific competition and predation between immature *Amblyseius fallacis*, *Amblyseius andersoni*, *Typhlodromus occidentalis* and *Typhlodromus pyri* (Acari: Phytoseiidae). *Exp. Appl. Acarol.* 19: 247-257.

Received for publication 6 December 1996; accepted 4 February 1998.